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TROPHIC INTERACTIONS AND CYCLIC POPULATION DYNAMICS OF THE AUTUMNAL MOTH: THE IMPORTANCE OF HYMENOPTERAN PARASITOIDS

by

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CONTENTS

1. INTRODUCTION

Among the most fascinating and widely studied phenomena in the field of ecology during recent decades have been fluctuations in population densities, in particular the periodic or quasi-periodic population cycles and regular or irregular outbreaks observed among many herbivorous mammal, bird and insect species. The classic studies by Charles Elton (1924, 1942) introduced population cycles to a larger group of ecologists and launched scientific research on the topic. Widely fluctuating numbers of herbivorous insects are particularly interesting, since many species – whether cyclically outbreaking, such as some moths, or irregularly outbreaking, including certain bark beetles and locusts – often constitute serious forest or agricultural pests. Thus their population cycles and outbreaks represent a conspicuous biological phenomenon which also has a sizeable economic impact. Furthermore, cyclic population dynamics are important issues in population ecology and form the basis of many theoretical models of present-day ecological studies. Against this background, it is not surprising that the causes underlying the population cycles of insects, as well as those of other cyclic herbivores (small rodents, hares and game birds), have been intensively debated for decades (e.g. Elton 1924, 1942, Krebs *et al.* 2001, Moss & Watson 2001, Berryman 2002, Turchin 2003, Korpimäki *et al.* 2004).

Ecological studies on herbivory as well as many other topics often consider only interactions between two trophic levels at a time: either between plants and herbivores or between herbivores and their natural enemies. Such an approach provides an important but nevertheless only partial view of communities, which largely involve at least three or four trophic levels (Price *et al.* 1980, Gomez & Zamora 1994, Schmitz *et al.* 2000). In order to understand biological systems as a whole, all trophic levels and interactions between them need to be taken into consideration.

1.1. Cyclic population dynamics

Both exogenous and endogenous factors are theoretically capable of generating regular population cycles. In the case of exogenous factors, such as climate and sunspot activity, populations directly follow the cyclic oscillation of the external variable (Myers 1998). Endogenous factors, in contrast, operate in a delayed density-dependent manner: a delayed negative feedback causes an oscillatory instability in the populations involved and eventually regular cycles for two or more interacting species emerge, provided that the effects of other factors, whether directly density-dependent or density-independent, are sufficiently weak.

Endogenous processes involve both self-regulating and trophic mechanisms (Berryman 2002, Turchin 2003). The self-regulating mechanisms of a population, i.e. phenotypic or

genotypic changes and maternal effects, can create the required time delays because the reproduction and/or survival of one generation is affected by the density of a previous generation (Krebs 1978, Ginzburg & Taneyhill 1994, Rossiter 1994, Berryman 2002). Trophic interactions between resource and consumer may be interactions between food plant and herbivore or between an herbivorous prey and its predator; the latter also include other natural enemies, such as parasites, parasitoids or pathogens. Such trophic interactions are nowadays the most widely studied mechanisms potentially causing herbivore population cycles (Haukioja 1990, 1991, Hudson *et al.* 1998, Klemola *et al.* 2000, 2003, Berryman 2002, Korpimäki *et al.* 2002, Turchin 2003), apart from the red grouse (*Lagopus lagopus scoticus* Latham), whose population cycles have been suggested to be driven by intrinsic male territoriality, possibly in conjunction with specialist parasitic worms (Watson *et al*. 1994, Mougeot *et al.* 2003, Seivwright *et al*. 2005). The plant-herbivore relationship may lead to population cycles through qualitative or quantitative changes in preferred food plants. Well-known examples of such interactions are the lowered nutritional quality of the host plant due to increased amounts of defensive secondary compounds, as a result of increasing grazing pressure by insect herbivores (Haukioja 1980, 1990, 1991), and the slow regeneration of the vegetation destroyed by lemmings in tundra ecosystems (Turchin *et al.* 2000, Turchin & Batzli 2001). On the other hand, the predator-prey hypothesis suggests that specialist and generalist enemies drive the population cycles of their prey (Anderson & Erlinge 1977, Anderson *et al.* 1980, Hansson 1987, Henttonen *et al.* 1987, Hanski *et al.* 1991, Klemola *et al.* 2002). Accordingly, specialist predators respond numerically to changes in prey density, because of their limited ability to switch to alternative prey species. The population dynamics of specialist enemies and their prey species are thus tightly coupled together. This may generate and maintain cyclic prey dynamics showing a delayed density-dependent pattern (May 1981), where the time-lag between prey and predator is due to the inherently slower population growth rate of predators compared to their herbivorous prey. In practice, however, most specialist-enemy-based mechanisms cannot sustain cyclic dynamics alone, without some direct density-dependent component provided by another factor, such as generalist enemies or a limited food supply (Hanski *et al.* 1991, Huitu *et al.* 2003). Without such regulation of the growth rate, herbivorous prey populations would escape from specialist enemy populations. Generalist enemies or food resources may thus shape the cyclic population dynamics, for example by maintaining low densities for a while, by slowing down the prey's population growth in the late increase and peak phases or even by preventing cycles from occurring in the first place (Hansson & Henttonen 1988). For the regular multiannual population cycles of herbivores, however, it is the delayed density-dependent (also called second-order) component that calls for explanation (Turchin & Hanski 2001). Generally speaking, there are a few main hypotheses put forward to explain the cyclic dynamics of herbivores. This brief summary does not allow full consideration of many species- or case-specific

modifications of the hypotheses. Interested readers may fill the gaps by consulting the references cited and other recent literature.

1.1.1. Cyclic population dynamics of the autumnal and winter moth

The autumnal moth, *Epirrita autumnata* (Borkhausen), and the winter moth, *Operophtera brumata* (Linnaeus) (both: Lepidoptera, Geometridae)] are univoltine and polyphagous moths found widely in the holarctic area (Tenow 1972). Both species show nine- to eleven-year population cycles, with occasional outbreak densities in northern and mountainous Fennoscandia (Tenow 1972). As has recently been observed in many regions of northern Finland, mountain birch *Betula pubescens* ssp. *czerepanovii* (Orlova) Hämet-Ahti forests may be severely defoliated over vast areas during these outbreaks, affecting the livelihood of the Sami people – whether traditional (reindeer herding) or modern (tourist industry).

The cyclic population dynamics of the autumnal moth have been intensively studied since the 1970s. Two main hypotheses, both acting in a setting of delayed density-dependence, have been proposed as the ultimate explanation of the cycles. Earlier studies have mainly focused on the hypothesis exploring the role of delayed inducible resistance (DIR) of birches (Haukioja *et al.* 1988, Neuvonen & Haukioja 1991, Kaitaniemi *et al.* 1999). The DIR hypothesis suggests that the increased consumption of mountain birches arising from a high population density of the autumnal moth has a delayed negative effects on their nutritive quality.

The alternative mechanism, which can be called the specialist parasitoid hypothesis, suggests that the cyclic population dynamics of the autumnal moth may be driven by hymenopteran parasitoids. This hypothesis has previously received less attention than that focusing on DIR (but see Ruohomäki 1994, Bylund 1995, Klemola *et al.* 2002, 2008, Tanhuanpää *et al.* 2002). Observational data on autumnal moth population dynamics suggest that hymenopteran parasitoids may play an important role in the system. First, the parasitism rates of the autumnal moth vary enormously depending on the cycle phase. Parasitism is virtually absent in the early increase phases, but proliferates in the peak and post-peak phases of the cycle, when the rates can be close to 100 % (Tenow 1972, Bylund 1995, Ruohomäki *et al.* 2000, **V**, K. Ruohomäki and T. Klemola unpublished data). Second, parasitism rates seem to follow the population densities of the autumnal moth at a time lag of two to three years (Bylund 1995, Tanhuanpää *et al.* 2002, **II**, **V**, **VI**, K. Ruohomäki and T. Klemola unpublished data), which is theoretically consistent with population cycles of nine to eleven years. In addition, parasitoids are thought to act as (functional) specialists in the system due to a lack of suitable alternative (geometrid) host species. Parasitoids are thus found to be theoretically and empirically capable of driving the population cycles of the autumnal moth due to a built-in delayed density-dependence (Klemola *et al.* 2002, Tanhuanpää *et al.* 2002).

Recently, Haukioja (2005) has put forward a novel hypothesis, combining mechanisms based on both plant quality and parasitism. He suggests that elevated inducible plant defences resulting from increased grazing pressure have a positive effect on the ability of herbivores to protect themselves against parasitoids (Haukioja 2005). Another possibility is that elevated inducible plant defences are related to the variation in ultraviolet B (UV-B) radiation, which is linked to sunspot cycles (Haukioja 2005). In these two scenarios, high grazing and/or UV-B triggers the octadecanoid defence pathway in birches, with a negative effect on the autumnal moth performance. This seems to trigger increased immune defence in the autumnal moth against parasitoids, which could explain the low parasitism rates in the increase phase of the cycle (Kapari *et al.* 2006). Nilssen *et al.* (2007), however, have recently shown that sunspot activity, with an eleven year cycle, cannot be the ultimate generator of the moth cycles of nine to eleven years. The scenario whereby inducible plant defences are combined with the impact of parasitoids through immune defence mechanisms remains to be scrutinized (see **VI**).

The role of epidemic diseases on the cyclic population dynamics of the autumnal moth has not been explicitly studied, but field observations suggest that diseases are only rarely involved in population declines (Tenow 1972, Ruohomäki *et al.* 2000, personal observations). In some other systems, macro- and microparasites may have crucial role on the cyclic population dynamics of the host species due to lowered reproduction and survival. Viral infection by the nucleopolyhedrovirus microparasite, for example, can be over 75 % in peak and declining populations of western tent caterpillars [*Malacosoma californicum pluviale* (Dyer)] suggesting the importance of diseases for the cyclicity of the species (Cory & Myers 2009).

The population cycles of the winter moth in Fennoscandia have been less widely studied than those of the autumnal moth (but see Tenow 1972, Tenow *et al*. 2007, Jepsen *et al*. 2008). There is, however, no fundamental reasons to assume that the population cycles of the winter moth are caused by other mechanisms than those suggested for the autumnal moth, although there may naturally be some species-specific attributes that are not yet well understood.

1.1.2. Synchronous or phase-lagged population cycles

Population cycles among and within lepidopteran species tend to be synchronous over large geographic areas, at least within a time window of a few years (e.g. Williams & Liebhold 1995, Myers 1998, Peltonen *et al.* 2002, Raimondo *et al.* 2004, Klemola *et al.* 2006). Intra-specific spatial synchrony and inter-specific temporal synchrony among populations may for example be affected by the weather. A specific mechanism whereby the weather synchronizes populations over a large scale is the Moran effect, according to which independent populations are synchronized by regionally-correlated environmental disturbances (Moran 1953, Royama 1992). Factors such as dispersal and trophic bottom-

up and top-down processes may cause smaller-scale patterns of spatial and temporal synchrony, respectively (Ranta *et al.* 1995a, b, Liebhold *et al.* 2004).

The population cycles of the autumnal and winter moth in northern Fennoscandia are phase-locked but often slightly phase-lagged. Peak densities first occur in the autumnal moth, followed by the winter moth at a time-lag of 1–3 years (Tenow 1972, Tenow *et al.* 2007, Klemola *et al.* 2008, **II**). The outbreak range of the winter moth has also recently spread from maritime to more continental areas, which earlier were typical of autumnal moth outbreaks only. The overlap in the current continental distributions has consequently already led to more intense and longer-lasting defoliations of mountain birch forests, since winter moth peaks lag behind those of the autumnal moth. In spite of increasing interest in this phenomenon (Tenow *et al.* 2007, Jepsen *et al.* 2008, Klemola T. *et al.* 2008), our understanding of the mechanisms underlying the phase-lagged population dynamics of the moth species remains poor. Klemola T. *et al.* (2008) suggested that either the host utilization of the most important parasitoids and/or pathogens or the inducible resistance of the host tree have to be strictly species-specific in order to produce the observed differences in population dynamics. Their study did not support the second hypothesis, while the role of natural enemies is still largely unknown (but see **II**).

The asynchronicity of the population dynamics could indeed be explained by predator/parasitoid-mediated mechanisms. Winter and autumnal moths are attacked, at least partly, by the same natural enemies, including generalist invertebrate and vertebrate predators as well as hymenopteran parasitoids; as already mentioned, the last-mentioned probably operate in this northern ecosystem as functional specialists in one or both moth species, due to the paucity of suitable alternative hosts. Generalist enemies, whose population densities do not follow those of the moths, have most pronounced effects on moth population dynamics during low-density phases of the cycle, whereas with increasing prey density in the high density phase of the cycle they become quickly saturated (e.g. Morris *et al.* 1958, Campbell & Sloan 1977, Holmes *et al.* 1979, Berryman *et al.* 1987, Berryman 2002, Enemar *et al.* 2004). Thus a preference by shared generalist enemies for one of the co-occurring moth species could delay the population increase of the preferred species in the early phases of the cycle. On the other hand, specialists, with their delayed density-dependent numerical response to changes in moth densities, affect prey species most in the late increase, peak and especially crash phases of the cycle (Berryman 2002, Turchin 2003). A preference or specialisation of enemies for one moth species over another may thus contribute to the earlier collapse of the preferred species (**II**).

1.2. Three trophic level interactions in the mountain birch – autumnal moth – parasitoid system

Populations of three trophic levels are affected by bottom-up forces (resource-limited systems) and/or top-down ones (enemy-limited systems). Different trophic levels, i.e. plants, herbivores and carnivores, are connected by a large number of direct and indirect interactions (Price *et al.* 1980, Schmitz *et al.* 2000, van Veen *et al.* 2006, 2008, Bukovinszky *et al.* 2008). Natural enemies, for example, may directly regulate herbivore numbers and thereby indirectly affect the feeding pressure encountered by plants. Interaction between plants and herbivores is assumed to be antagonistic, but sometimes herbivore damage can benefit the plant by overcompensation resulting for example from the release of apical dominance (see Agrawal 2000).

Complex trophic cascades may be associated with the chemical ecology of the host plant (Walker & Jones 2001), either via host plant quality for the herbivore (Duffey 1970, Campbell & Duffey 1981; see section 1.2.1.) or via host plant volatiles (Turlings *et al.* 1990, 1991). In the latter case, leaf consumption by herbivores induces a chemical reaction in the host plant and leads to the release of inducible volatile organic compounds (VOCs) (Turlings *et al.* 1990, 1991, De Moraes *et al.* 1998, Turlings & Wäckers 2004, Heil 2008). VOCs can be used by predators and parasitoids in their search for prey (e.g. Camors & Payne 1972, Price *et al.* 1980, Nealis 1986, Turlings *et al.* 1990, De Moraes *et al.* 1998, Halitschke *et al.* 2008). Thus they may contribute to reducing herbivore pressure on the host plant (van Loon *et al.* 2000, Kessler and Baldwin 2001, Heil 2008). This phenomenon is often referred to as 'crying for help'. Such complex interaction between plants and the third trophic level, however, should be advantageous for the host plant only if natural enemies are able to sufficiently reduce herbivore pressure, to outweigh the obvious costs of chemical signalling (van der Meijden & Klinkhamer 2000, Fritzshe Hoballah & Turlings 2001, Hoballah *et al.* 2004).

1.2.1. Three trophic level studies from an immunoecological perspective

The insect cuticle forms a first barrier against enemies, but if it is penetrated by a parasite or pathogen, the insect's immune system is activated. The process begins with the recognition of a foreign antigen and eventually leads to exocytosis and to the release of coagulation-, recognition-, growth- and opsonin-like factors (Hoffmann 1995, Kanost *et al.* 2004, Iwanaga & Lee 2005). The activation of further defence responses leads to opsonisation, phagocytosis and the production of melanin (i.e. the encapsulation reaction), which is primarily responsible for the killing of parasitoid eggs (Gillespie *et al.* 1997, Lavine & Strand 2002). Bacteria, fungi or viruses, on the other hand, mainly activate the insect's humoral defence system, leading to the production of soluble antimicrobial, antifungal and antiviral proteins and molecules including the phenoloxidase enzyme (PO enzyme) (Gillespie *et al.* 1997, Lavine & Strand 2002). Estimation of the encapsulation

reaction against foreign antigens and of PO enzyme activity from insect haemolymph are widely used methods for describing the level of immune defence of an insect.

The insect immune system is partly genetically determined, but it may also be affected by other factors, including food quantity and quality as well as population density (e.g. Reeson *et al.* 1998, Adamo *et al.* 2001, Cotter *et al.* 2004). For example, host plant quality has an obvious effect on the herbivore performance and fitness due to variations in the composition of nutritional and defensive compounds of the plant (Price *et al.* 1980), but interactions operating via host plant quality may also affect the third trophic level by influencing herbivores' ability to defend themselves against enemies (e.g. Ojala *et al*. 2005, Lee *et al.* 2008, Povey *et al*. 2009). Since the activation and maintenance of the insect immune system is costly (Schmid-Hempel 2005, Siva-Jothy *et al.* 2005, Sadd & Schmid-Hempel 2009), individuals presumably also need a high quality diet to achieve an effective immune defence against their enemies.

Ecological studies on invertebrate immunology have commonly focused on questions within the field of evolutionary ecology, such as sexual selection (Rolff & Siva-Jothy 2003, Schmid-Hempel 2003). Less attention has been paid to studying the relationship between immunology and population ecology, although natural enemies have population-level impacts on host species by directly affecting their survivorship as well as fecundity. For example, insects in crowded conditions are thought to invest relatively more in their immune function, as the risk of parasitism and pathogen infections increases. This has been termed the hypothesis of density-dependent prophylaxis (DDP) (Goulson & Cory 1995, Reeson *et al.* 1998, Wilson & Reeson 1998). Investment in immunity, however, may lead to a reduction in other performance, such as growth and fecundity (Sheldon & Verhulst 1996, Moret & Schmid-Hempel 2000, Adamo *et al*. 2001), thus having population-level consequences as well. DDP against parasitoids and pathogens should be manifested particularly in cyclic insect species, such as autumnal and winter moths, whose populations occasionally achieve extremely high densities. Indeed, field observations have revealed a clear reduction in size and fecundity during the increase phase of the autumnal moth (Klemola *et al.* 2004, 2008) possibly resulting, at least in part, from the trade-off between growth and immune defence under crowded conditions (Klemola *et al.* 2004).

Insects are capable of defending themselves against natural enemies, for example by destroying parasitoid eggs or neonate larvae through cellular encapsulation. Thus, koinobiont parasitoids, which allow their insect hosts to feed and grow in size after parasitism, must endure complex host-defence reactions (Godfray 2000, Pennacchio & Strand 2006, Sadd & Schmid-Hempel 2009). But parasitoids are also not unarmed against their hosts' immune defence. For example, they can inject viruses and virus-like particles (e.g. poly- and non-poly-DNA viruses) (Glatz *et al.* 2004, Lawrence 2005) as well as

venom (Richards & Parkinson 2000) into the host in order to suppress host immunity. Thus host resistance experiments with natural enemies are recommended, taking into account the complexity of interactions between host and natural enemy (Adamo 2004, Sadd & Schmid-Hempel 2009).

1.3. Aims of the thesis

First and foremost, this doctoral thesis investigates the effects of natural enemies, especially hymenopteran parasitoids, on the population dynamics of the autumnal moth (**I, II, VI**). One of the main aims was to obtain experimental evidence for the specialist parasitoid hypothesis, governing the observed cyclic dynamics of the autumnal moth (**I**). Since a parasitoid (predator) exclusion experiment is obligatory in confirming the role of specialist enemies on the cyclic population dynamics of the host species, three different experimental settings were established: parasitoid-proof cages (closed cages), open cages permeable to parasitoids and control plots. The prediction was that the reduction in mortality due to parasitoid removal would lead to an autumnal moth abundance that would remain high longer in closed cages than in open cages or control plots. This would eventually result in small-scale outbreak densities and conspicuous birch defoliation of autumnal moth larvae; in the other treatments, in contrast, autumnal moth densities would collapse sooner and concurrently with local autumnal moth density due to the action of parasitoids.

The effects of shared natural enemies, including both generalists and specialists, were examined as possible explanatory mechanism for the phase-lagged population dynamics of the autumnal and winter moths (**II**). Specifically, the efficiency and preference of larval and pupal parasitoids as well as those of vertebrate and invertebrate pupal predators were examined experimentally under field conditions. Based on the field data, a new hypothesis was formulated to explain the seemingly phase-lagged population dynamics of the autumnal and winter moth.

Some of the assumptions of the hypothesis of Haukioja (2005), combining the effects of the two predominant mechanisms, i.e., DIR and specialist parasitism, on the cyclicity of the autumnal moth, were also tested in the field (**VI**). This study examined the possible effect on parasitoid performance of inducible plant defences triggered by autumnal moth grazing. According to Haukioja (2005), inducible plant defences triggered by autumnal moth grazing should have a positive effect on the immune ability of herbivores to protect themselves against parasitoids. Specifically, this possibility was studied by collecting autumnal moths from several different locations with different current and past population densities. The immune response (encapsulation reaction, see *2.3.6.*) against an artificial antigen, and vulnerability to real natural enemies in the field, were

examined. Populations which confronted a stronger grazing pressure were assumed to benefit more in terms of increased immune defence against natural enemies.

One of the aims of this thesis was to explain more specifically the complex interactions occurring between the three trophic levels in the system. One was whether hymenopteran parasitoids could benefit plants not only by killing herbivorous insects (and reducing future herbivore pressure), but also by reducing immediate feeding pressure from herbivores (**III**). Decreased feeding by herbivores could provide an explanation for the advantageous use of VOCs by plants.

The connective mechanism between the three trophic levels may also operate via host plant quality, either via natural host plant quality, i.e. constitutive nutritional quality (**IV, V**) or via specific inducible resistance (**VI**). The relationship between food plant quality and immune defence against parasitoids was experimentally examined both in the laboratory (**IV**) and in the field (**V**). As already noted, in all studies where a component (i.e., encapsulation ability) of the immune response of the autumnal moth was measured (**IV–VI**), the linkage between the first and third trophic level was predicted to operate via the herbivore's immune defence against parasitoids.

Immune defence was determined by measuring the encapsulation reaction of autumnal moth pupae against an artificial antigen in the laboratory. In one study, the phenoloxidase (PO) activity of the pupal haemolymph was also measured (**IV**). However, it is not yet known how well the encapsulation response corresponds to the vulnerability of autumnal moths to naturally occurring parasitoids. In order to ensure the biological and particularly the population-level significance of the methods used, the host resistance experiments were therefore conducted by exposing autumnal moth larvae and pupae to wild hymenopteran parasitoids in the field (**V, VI**).

2. MATERIAL AND METHODS

2.1. Study areas

The studies included in this thesis were conducted at the Kevo Subarctic Research Station of the University of Turku in northern Finland (69°45'N, 27°01'E) (**I–VI**), at Skippagurra in northern Norway (70º09'N, 28º13'E, 65 km NE of Kevo) (**II**, **V**, **VI**), and at Hana in northern Norway (70º14'N, 28º27'E, 80 km NE of Kevo) (**II**, **V**, **VI**). For the purposes of study **VI**, autumnal moth larvae were also sampled at seven other sites in northern Finland and Norway (see Fig. 1. in **VI** for further details). The study sites were dominated mainly by mountain birch forest (average height about 2–5 metres), along with dwarf shrubs [mainly *Vaccinium myrtillus* L., *V. uliginosum* L. and *Empetrum nigrum* L. ssp. *hermaphroditum* (Lange ex Hagerup) Böcher]. Detailed characteristics of the study sites are given in the published articles and manuscripts **I–VI**.

2.1.1. Natural autumnal and winter moth densities

Clearly phase-lagged population cycles for autumnal and winter moths were observed at all study sites during the studies. Peak phases of the autumnal and winter moth cycles (without outbreak densities) were achieved at Kevo in 2004 and 2005, respectively. Thereafter, the larval densities for both species started to decrease, ending up at extremely low densities in 2007 and 2008. At Skippagurra, outbreak densities were first achieved by autumnal moths in 2003–2005, and then by winter moths in 2006. At Hana, severe outbreak densities and almost total defoliation of the mountain birch forest were observed for autumnal moths in 2002 and 2003 (Klemola *et al.* 2008, **VI**). In 2004, the autumnal moth density at Hana had already started to decrease, reaching practically zero density in 2007. The winter moth was rare at Hana until 2004, after which its density increased strongly, peaking in 2006 but with still a relatively high density in 2007 and 2008 (Klemola *et al.* 2008). A similar pattern in population dynamics, but at non-outbreak densities (an order of magnitude lower), was also observed over large areas in northernmost Finland (**VI**). It is typical of both moth species that the cyclic peak can occur either with or without true outbreak densities or visible damage to mountain birch forests.

2.2. Study species

2.2.1. The mountain birch as a host for the autumnal moth

The mountain birch is an introgressive hybrid of dwarf birch (*Betula nana* L.) and downy birch (*Betula pubescens* Ehrh.) (Vaarama & Valanne 1973). The mountain birch

phenotype is highly variable, ranging from small bushes, over short polycormic trees, to taller monocormic trees. In northern Fennoscandia, the mountain birch forms the tree line and is the main host tree of autumnal and winter moths. Mountain birches differ widely in their food quality for insect herbivores. This is due to differences in nutritive factors (e.g. sugars, proteins and fatty acids), foliar water content, leaf toughness, and multiple putative defence compounds (secondary defence compounds such as tannins and other phenolic compounds) as well as specific defence cascades such as octadecanoid signaling and the salicylic acid pathway (Haukioja 2003, 2005). The quality of the mountain birch influences the growth, behaviour and survival of the autumnal and winter moth. The reproductive capacities of the moths, which also primarily depend on the quality of food accumulated during the larval stage, are measured accurately as pupal mass (Haukioja & Neuvonen 1985, Tammaru *et al.* 1996a, b, Heisswolf *et al.* 2009, **II**).

Numerous studies on the quality of mountain birch foliage for the autumnal moth have been conducted over the last three decades at the Kevo Subarctic Research Station. It has nevertheless proved impossible to identify a single compound primarily affecting host plant quality, due to the complexity of interactions among different compounds and changes in leaf chemistry over the summer (Riipi *et al.* 2002, 2004, Haukioja 2003, 2005). If we want to measure a single leaf trait as a proxy for leaf quality for the autumnal moth, however, it should be the leaf-water content, which is correlated with leaf phenology and with the accompanying chemical and physiological changes in leaves (Haukioja 2003, 2005, Henriksson *et al.* 2003). Another trait frequently used to describe qualitative differences between mountain birches as larval food is the autumnal moth pupal mass, due to its strong correlation with potential fecundity (see above).

2.2.2. The autumnal moth and the winter moth

Both the autumnal and the winter moth are described in detail in the original articles and manuscripts included in this thesis (**I–VI**). To summarize the main points; in the spring, the overwintered eggs of both moths hatch concurrently with mountain birch bud-break. The larvae go through five larval instars. Autumnal moth larvae feed freely on the leaves of the mountain birch, whereas winter moth larvae often live between leaves loosely spun together. The autumnal moth is larger and typically one larval instar ahead of the winter moth in development. Autumnal moths also pupate in the soil about a week earlier than winter moths (Mjaaseth *et al.* 2005). Emergence of autumnal moth adults begins in mid-August onwards, while winter moth adults eclose a few weeks later. In both species, adults rely solely on larval-derived resources and do not feed for maintenance or reproduction. Autumnal moth females are considered relatively poor fliers (Ruohomäki *et al.* 2000), while wingless winter moth females are totally flightless.

2.2.3. Natural enemies

Winter and autumnal moths are attacked at least in part by the same natural enemies, including invertebrate and vertebrate predators as well as hymenopteran parasitoids. Predators such as ants, beetles, spiders, insectivorous birds and small mammals (voles and shrews) are thought to act as generalists in the system (Tanhuanpää *et al.* 1999, 2001, Ruohomäki *et al*. 2000, Klemola *et al.* 2002, Enemar *et al.* 2004, Hogstad 2005, **II**).

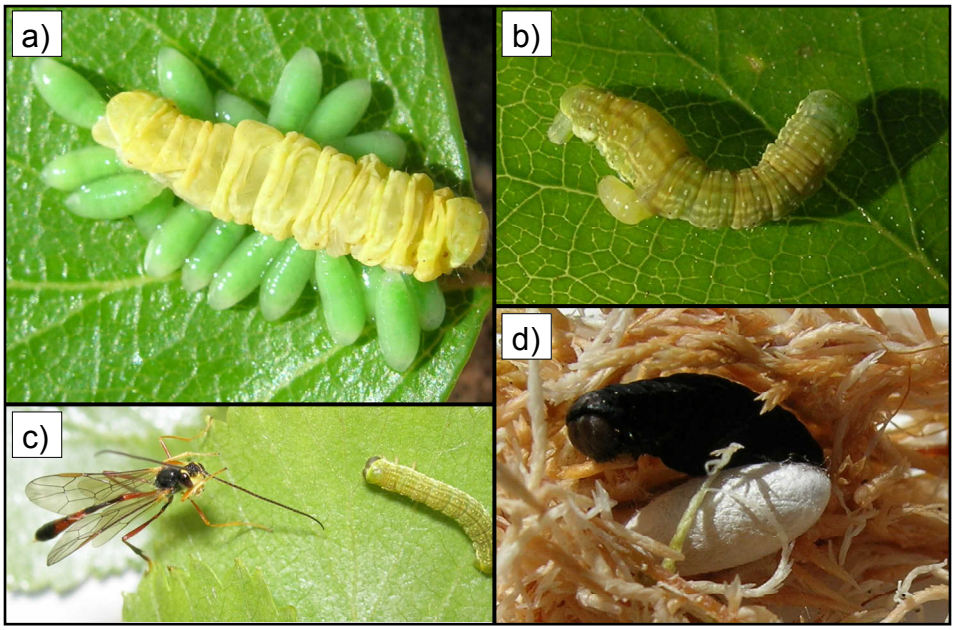

Figure 1. a) *Eulophus larvarum* larvae (the only gregarious ectoparasitoid found to parasitize autumnal and winter moths) sucking an autumnal moth larva. b) A parasitoid larva, either *Protapanteles anchisiades* or *Cotesia salebrosa*, emerging from an autumnal moth larva. c) An *Agrypon flaveolatum* female attacks an autumnal moth larva. d) *Zele deceptor* has pupated next to a partially consumed, dead autumnal moth larva. Photos by Tero Klemola (a, b), Netta Klemola (c) and Tea Ammunét (d).

Parasitoid wasps (insects whose larvae have to develop within or on the body of another insect, although the adults are free-living) are considered to act as specialists for the autumnal moth due to the lack of alternative suitable host species in northern Fennoscandia, at least before the recent spread of the winter moth (Ruohomäki *et al.* 2000, Klemola *et al.* 2002, **II**). According to long-term studies at Kevo and other locations in northern Fennoscandia, parasitoid species attacking either the autumnal or winter moth or both include at least one egg species, some fifteen larval species, at least one larval-pupal species and some five pupal species (Ruohomäki 1994, Ruohomäki *et al.* 2000, **II**, **V**, **VI**). The hymenopteran parasitoids observed during this four-year thesis project and thus mentioned in the original articles are listed in Table 1. Figure 1 shows some of the most common parasitoid species of the autumnal moth.

Table 1. Hymenopteran parasitoids reared from autumnal moth eggs, larvae and pupae in the four-year thesis project (see also Ruohomäki 1994, Kaitaniemi & Ruohomäki 1999, **I–III**, **V**, **VI**). The table shows parasitoid guild (egg, early larval, late larval or pupal parasitoid), species, family [Ichneumonidae (Ich), Braconidae (Bra), Eulophidae (Eul) or Scelionidae (Sce)], as well as type of the parasitoid [solitary (S), gregarious (G), endoparasitoid (Endo) or ectoparasitoid (Ecto)]. All larval parasitoid species are koinobionts, i.e. they allow the host larva to feed and continue its development until it is eventually killed.

Name	Family	Type	Winter moth[a]
Egg parasitoids			
Telenomus cf. *laeviceps* Förster	Sce	S, Endo	Yes
Early larval parasitoids			
Protapanteles anchisiades (Nixon)	Bra	S, Endo	Yes
Cotesia salebrosa (Marshall)	Bra	S, Endo	Yes
Phobocampe[b] sp. Förster	Ich	S, Endo	Yes
Aleiodes cf. *gastritor* (Thunberg) agg.	Bra	S, Endo	No
Late larval parasitoids			
Eulophus larvarum (Linnaeus)	Eul	G, Ecto	Yes
Zele deceptor (Wesmael)	Bra	S, Endo	No
Campoletis varians (Thomson)	Ich	S, Endo	No
Agrypon flaveolatum (Gravenhorst)	Ich	S, Endo[c]	Yes[d]
Pupal parasitoids			
*Cratichneumon viator (*Scopoli)	Ich	S, Endo	Yes
Pimpla flavicoxis Thomson	Ich	S, Endo	Yes
Unidentified (Subfamily Ichneumoninae)	Ich	S, Endo	Yes

[a] 'Yes': the species is known also for the winter moth in northern Fennoscandia (own observations, observations of co-authors and communications from Rolf A. Ims and Tino Schott at the University of Tromsø, Norway).

[b] The most common species was probably *Phobocampe tempestiva* (Holmgren) (communications from Anu Veijalainen and Ilari E. Sääksjärvi at the Zoological Museum of the University of Turku, Finland).

[c] Larval-pupal parasitoid

[d] *A. flaveolatum* did not parasitize winter moths in my studies, but is known to do so in NW Norway (near Tromsø) and in other areas in Europe and North America (**II**).

2.3. Experimental procedures

Here only brief descriptions of the experiments conducted are given. The methods are described in detail in the Material and Methods -sections of the articles and manuscripts (**I–VI**).

2.3.1. Experimental larvae

The parents of experimental autumnal moth larvae were obtained from the wild in the preceding summer or from cultures maintained for 1–2 generations at the Kevo Subarctic Research Station and mated in the laboratory. For the purposes of study **VI**, fifth instar autumnal moth larvae were collected from ten sampling sites located in the vicinity

of Kevo (1.2–80 km from Kevo; see Fig. 1 in **VI**). For study **II**, winter moths were collected from the wild as first and second instar larvae (Nuorgam, northern Finland, 70º04'N, 27º52'E).

2.3.2. Study trees

For the purposes of immunoecological studies **IV** and **V**, experimental trees were chosen based on their quality for herbivores. In these studies, tree classification (high or low quality tree) was based on the earlier performance of autumnal moth larvae on those trees. The indices for leaf quality included relative larval growth rates (RGRs) in short-term growth experiments in the laboratory (**IV**, **V**), as well as the pupal masses of individuals reared in mesh bags on the trees throughout the larval stage (**V**).

2.3.3. Estimation of larval and pupal parasitism and pupal predation

Rates of larval parasitism were estimated by collecting either wild (**II**, **V**, **VI**) or introduced (**II**, **V**) larvae. The larvae were transported to the laboratory and reared individually in vials (48 ml). They were fed with fresh mountain birch leaves and checked for possible parasitoid emergence approximately every second or third day. Prepupating larvae were allowed to pupate inside vials filled with moist *Sphagnum* moss. After 7–10 days, individuals were checked again for parasitoids emerging from the prepupae (*Z. deceptor* and *C. varians*). The remaining pupae were kept in a refrigerator until the spring, after which the fates were checked again for parasitoids emerging from the pupae (*A. flaveolatum*).

Figure 2. A plastic cage filled with moss and used in pupal predation and parasitism experiments in the field. Photo by Tero Klemola.

For the purposes of studies **II**, **V**, **VI** , pupae were exposed to pupal predation and parasitism inside small open-topped plastic cages (6 × 3 × 4 cm with 0.5 cm mesh; Figure 2), which were filled with moist *Sphagnum* moss. The cages were buried a few centimetres deep in the moss layer. After field exposure the pupae were transported back to the laboratory, where their fates (surviving, predated, parasitized) were checked.

2.3.4. Parasitoid exclusion experiment

The parasitoid exclusion experiment (**I**) started in the summer of 2006 and lasted three years. Three treatments were established: 1) the 'closed cage' treatment, where all natural enemies were excluded (Figure 3a); 2) the 'open cage' treatment, with free entrance to all egg, larval and pupal parasitoids (as far as it is known, there are no flying generalist predators in the study area that could have entered the open cages and caused mortality losses there) (Figure 3b); and 3) the 'no cage' treatment, representing control plots, where free access was possible for all specialist and generalist natural enemies. Founder autumnal moth larvae were introduced into the cages and control plots in early summer 2006, and no additions were made in any later stage of the experiment.

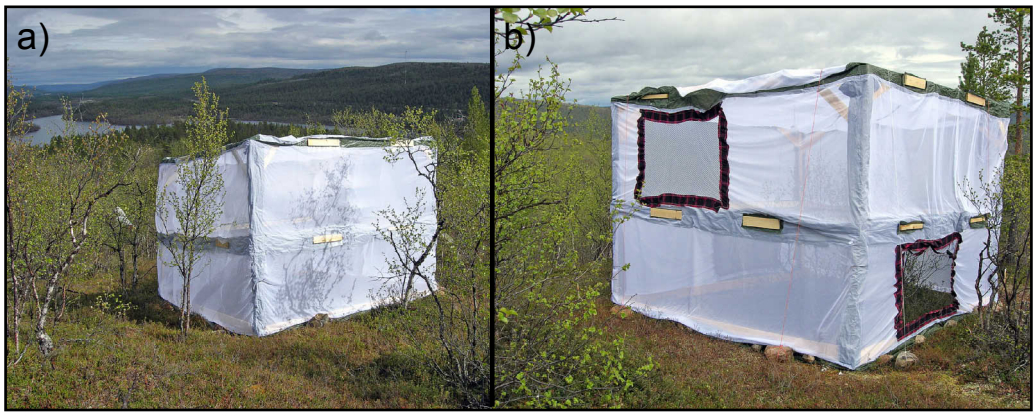

Figure 3. a) A parasitoid-proof closed cage; b) an open cage with parasitoid-permeable windows. The size of cages was 4 × 4 × 3 metres. Photos by Tero Klemola.

The abundances of autumnal moth larvae and adults were recorded throughout the whole study period. Larval abundances were estimated weekly each summer by counting all individuals on previously selected branches. The numbers of short shoots on these branches were also counted, and a common larval abundance index, i.e. the number of larvae found per 100 short shoots, was calculated. Once a summer the larval abundances were estimated visually, in order to access possible outbreak densities. The number of larvae found per unit time was counted and an index of relative larval abundance per ten minutes was calculated. The threshold used to distinguish outbreak from non-outbreak densities was 100 larvae per 10 min search, since at this density clear defoliation of the mountain birches has occurred (Klemola *et al.* 2008, **VI**). Adult abundances were estimated once a week in each study autumn by counting all adults found resting on the

trees or structures of the cages. Adult estimation was conducted in all cages but not in the control plots.

2.3.5. Feeding intensity of parasitized larvae

For the purposes of study **III**, both the daily food consumption and the duration of the 5th larval instar were measured for parasitized and unparasitized larvae in a controlled experimental setup in the laboratory. One group of autumnal moths was exposed to parasitisation by the solitary endoparasitoid *Z. deceptor*, while another group was treated as a control. Larval feeding was followed during ten days of the controlled feeding experiment, after which all experimental larvae had finished feeding and entered the prepupal stage. The leaf consumption of the larvae was estimated daily by measuring the difference in leaf area before and after approximately 24 hours of feeding from photographs of the leaves taken before and after feeding.

2.3.6. Immunoecological studies

The immune response of autumnal moths was determined from the pupae by measuring the encapsulation reaction to a foreign antigen (**IV**–**VI**) and the PO activity of the pupal haemolymph (**IV**). In order to measure the encapsulation reaction, an artificial 'parasite egg', i.e. a nylon monofilament 2 mm in length, was inserted into the pupal abdomen (Figure 4). The pupal immune system was allowed to react to this object, which after the implant was removed, dried and frozen. The nylon monofilament was then photographed from two angles to obtain the grey-value of the implant. The average grey-value of the two pictures was used; the higher the grey-value found the darker the implant, implying a high encapsulation ability (Figure 5).

To confirm the biological significance of the immunoassays, host resistance experiment with natural enemies were conducted. For this purpose, autumnal moth larvae and pupae were exposed to hymenopteran parasitoids in the field (**V**, **VI**).

Figure 4. An artificial antigen inserted into an autumnal moth pupa. Photo by Netta Klemola.

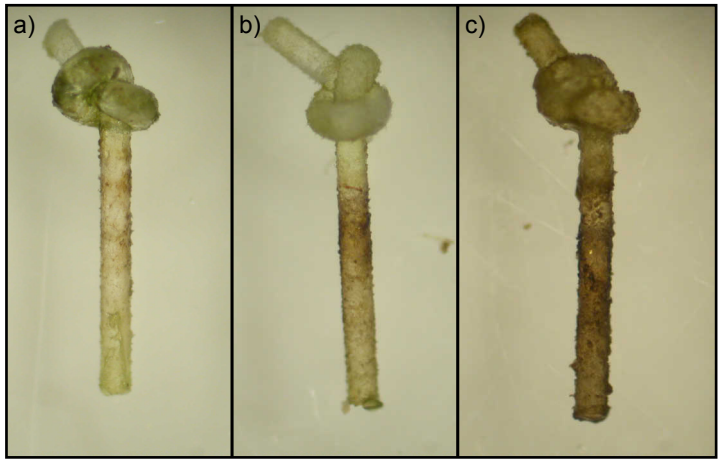

Figure 5. Examples of encapsulation reactions of autumnal moth pupae to a foreign antigen. a) A relatively light (111 grey value units) nylon monofilament, reflecting low encapsulation ability, b) an intermediate (140 units) monofilament, c) the darkest monofilament (187 units) reflects high encapsulation ability. Photos by Netta Klemola.

3. RESULTS AND DISCUSSION

3.1. Impact of hymenopteran parasitoids on the population cycles of the autumnal moth

The three-year-long exclusion of hymenopteran parasitoids led to a significant increase in the abundance of autumnal moth larvae in experimentally established populations of closed cages (**I**). As predicted by the specialist parasitoid hypothesis, larval abundances rose to a higher level and remained there longer in the closed cages than in the open cages or the control plots. Autumnal moth abundances in the open cages and control plots collapsed sooner, corresponding closely to the general decline of autumnal moth densities in the study area.

The observed differences between the treatments can be explained by the action of hymenopteran parasitoids. In the first study year, the mortality caused by larval parasitoids in the observational sample was almost 100 % (see Fig. 1 in **I**). This probably explains why the larval numbers in the unprotected control plots and open cages collapsed congruently with natural autumnal moth density. In contrast, larvae inside the closed cages were protected against parasitoid caused mortality, and larval numbers either continued to increase or remained at the same level throughout the three-year study.

This experimental study provided more support for the specialist parasitoid hypothesis, by suggesting that the population cycles of the autumnal moth may result from its interaction with natural enemies, especially hymenopteran parasitoids. The results clearly demonstrate that parasitoids play a role in the system, as already suggested by observational data (Bylund 1995, Klemola *et al.* 2008). Natural enemies are also thought to be important in other systems involving cyclic insect or mammal herbivore species. Good examples are the parasitoids affecting the population dynamics of the larch budmoth (*Zeiraphera diniana* Guenée) in Swiss Alps (Delucchi & Renfer 1977, Delucchi 1982, Turchin 2003); the impact of the clerid beetle [*Thanasimus dubius* (Fabricius)] on southern pine beetle (*Dendroctonus frontalis* Zimmermann) populations in the southern United States, Mexico and parts of Central America (reviewed in Reeve *et al*. 1995, Turchin 2003) and the impact of mammalian and avian predators on cyclic voles in Fennoscandia (Korpimäki & Norrdahl 1998, Klemola *et a*l. 2000, Korpimäki *et al*. 2002).

The results, however, were not totally unambiguous: larval abundance in one of the two closed cages remained relatively low, but at a constant level. Unfortunately, the harsh weather conditions in northern Fennoscandia made it difficult to construct more parasitoid-proof cages to increase the numbers of replication units in the study. This inconclusive nature of the results may also arise from the ecological fact that there are yet more factors involved in population dynamics of the autumnal moth. The present results do not for example resolve the question whether the tritrophic interaction between mountain birch,

herbivore and natural enemies offers a more plausible explanation of the cyclical dynamics than two simpler hypotheses, as, in fact, might be the case with the cyclic larch budmoth. Two main hypotheses, both acting in a delayed density dependent manner, have been put forward to explain the population cycles of the larch budmoth. The first one is based on changes in the food quality of the host tree, the larch (*Larix decidua* Mill) (Baltensweiler 1993). Larch trees suffering from defoliation lack nutrient resources, leading to low-quality needles for several consecutive years. The other hypothesis advocates the importance of parasitoids (Delucchi & Renfer 1977, Delucchi 1982). Recent empirical and modelling analyses suggest that a tritrophic explanation, combining both hypotheses, might best explain the cyclic dynamics of this species (Turchin 2003).

To conclude: empirical observations of parasitism together with modelling approaches have already provided a framework in which delayed density-dependent mortality due to parasitism has been seen as a driver of regular population cycles of the autumnal moth in northern Fennoscandia. Now that previous observations and theoretical work can be combined with the first experimental results, the view of the importance of hymenopteran parasitoids is further strengthened.

3.2. Combined effects of generalist and specialist natural enemies on phase-lagged population dynamics of the autumnal and winter moth

Study **II** showed opposite impacts of larval parasitoids and invertebrate pupal predators on autumnal and winter moths, thus providing a potential explanation for the observed phase-lagged population dynamics of the two moth species (Figure 6). The other factors examined, such as mortality caused by pupal parasitoids or vertebrate predators and differences in reproductive capacity, did not differ between the two moth species and seemed unlikely to be the cause of the observed phase-lag.

A potential mechanism for the phase-lagged population dynamics of autumnal and winter moths is provided by generalist invertebrate predators, which preyed three times more on winter moth pupae than on autumnal moth ones. In general, generalist predators have been suggested to have the most pronounced effect on cyclic prey species in the low density phases of the cycle (Andersson & Erlinge 1977, Erlinge *et al.* 1983, Hanski *et al.* 1991, 2001). The asynchrony between the two moth species may thus be strengthened by the different population growth rates resulting from varying mortality due to invertebrate predators in the early increase phase of the cycles (Figure 6).

The preference of specialist larval parasitoids provides a second possible candidate mechanism for the phase-lagged moth cycles. Specialists, whose population dynamics are tightly coupled with the moth cycles, preferred the autumnal moth over the winter moth and might thus cause the earlier collapse of the former (Figure 6). Indeed, in 2005 larval

parasitoids caused about 30 % mortality in autumnal moths at Hana. At the same time, the population density of this species started to decrease. In contrast, the larval parasitism rate for winter moths was zero and its density was still increasing during that year. In the actual study year 2007 at Kevo, larval parasitoids likewise parasitized three times more autumnal than winter moths. The differences in larval parasitism rates seemed to result mainly from the action of two parasitoid species, *Zele deceptor* and *Agrypon flaveolatum*. *Z. deceptor* was the dominant parasitoid species in 2005 at Hana, while *A. flaveolatum* caused the most interspecific differences in larval parasitism two years later in Kevo. In subsequent laboratory tests, both of these species appeared to be specialists for the autumnal moth (see also Table 1), although *A. flaveolatum* has been successfully used as a bio-control agent against winter moths in Canada (e.g. Roland & Embree 1995).

To conclude: the inverse effects of specialist and generalist natural enemies may provide a potential explanation for the observed phase-lagged population dynamics of winter and autumnal moths. Since the effect of larval parasitoids on the cyclic population dynamics of the prey is most pronounced in the peak and post-peak phases of the cycle, their preference for the autumnal moth may contribute to the earlier collapse of the autumnal moth cycle (Figure 6). Furthermore, the phase-lag may be strengthened by the action of generalist invertebrate predators at the low phase of the moth cycle, as they preferred the winter moth over the autumnal moth (Figure 6). Longer-lasting field studies, however, are still needed, as is the mathematical modelling of this hypothesis.

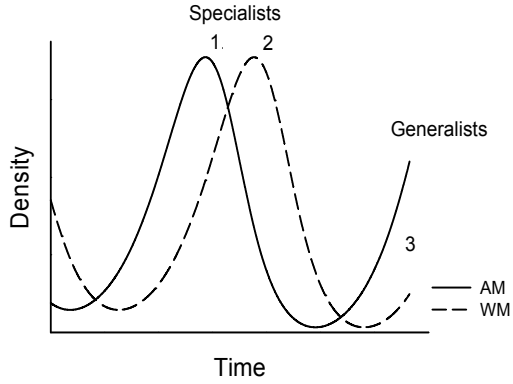

Figure 6. Graphic illustration of a possible mechanism whereby the reverse impacts of specialist and generalist natural enemies on two cyclic prey species could lead to the phase-lag in population dynamics. Hypothetical population cycles for the autumnal (AW) and winter (WM) moth are shown. Specialist enemies exert the most pronounced effect on the density of their prey at the peak and post-peak phases of the cycle. In our empirical study, specialists preferred the autumnal moth over the winter moth and thus may cause the earlier collapse of autumnal moth population density (timepoint 1 in the figure). In subsequent years, the winter moth would be the only abundant species in the system, and natural enemies would focus on attacking it, finally leading to a collapse in the winter moth population density also (timepoint 2). The effect of generalists is strongest at the low-density phase of the prey cycles. Our findings that generalist pupal invertebrate predators preferred the winter moth over the autumnal moth may strengthen the asynchrony between the cycles by causing a slower population growth rate for the winter moth at the low-density phases of the cycle (timepoint 3).

3.3. Effect of larval parasitism on food consumption of the autumnal moth

The main result of study **III** was that an increase in the parasitism rate can reduce herbivore pressure on the host plant, as parasitized 5th instar autumnal moth larvae consumed on average one mountain birch leaf less per individual than unparasitized larvae (i.e. parasitized larva consumed approximately 30 % less leaves than unparasitized one). Extrapolating the results to larval densities and parasitism rates observed in the field showed that parasitism can lessen leaf damage at low larval densities met in the low phase of the cycle. Parasitism is also able to prevent total defoliation of the host tree at intermediate larval densities during the decline phase of the cycle. When larval densities are extremely high or even at outbreak levels, parasitism is no longer sufficient to prevent total defoliation of the host tree. However, since outbreak larval densities are met only occasionally in some autumnal moth populations (e.g. **VI**), the ecological significance of the parasitoid attraction for the host plant seems obvious.

Parasitism was also found to reduce the developmental time of the autumnal moth larva, as parasitized larvae commenced pupation approximately one day before unparasitized ones. This may benefit not only the host tree but also the parasitoids themselves, in many ways. Firstly, it reduces the risk of feeding on decaying and infected tissue (Godfray 1994, but see Slansky 1986, Harvey 1996, van der Mejden *et al.* 2000) as well as the disadvantages resulting from toxic compounds originating from the host plant (Slansky 1986, Haukioja *et al.* 1988, Haukioja 2003). In addition, rapid pupation into the soil may reduce the risk of predation as well as hyper- and superparasitism (Abrams & Rowe 1996, Tanhuanpää *et al.* 1999, Harvey & Strand 2002). For example, pupal parasitism and predation rates are often relatively low compared to those of the larvae (Tanhuanpää *et al.* 1999, 2001).

Attracting parasitoids may be an important part of host plant protection against its herbivores, but parasitoids themselves evidently benefit from the chemical communication between the two trophic levels. However, further studies are needed, in particular to investigate the attractiveness of herbivore-induced mountain birch VOCs for parasitoids of the autumnal moth. It is also unclear whether plants, or birches in particular, have adapted to attract parasitoids, or whether parasitoids have merely learned to use chemical cues (e.g. by-products of some other function) from the host plants of their preferred insect hosts.

3.4. Food quality and immune defence against hymenopteran parasitoids

The relationship between host plant quality and a herbivore's ability to defend itself was examined in both laboratory and field conditions (**IV**–**VI**). Mountain birch quality had a significant effect on the immune defence of the autumnal moth both in the laboratory

and in the field, at least when measured by the encapsulation reaction against an artificial antigen. The results of laboratory and field studies, however, were quite contradictory. In the laboratory, low food quality led to a higher encapsulation response of the autumnal moth compared to individuals fed on high quality food. Field studies, which were repeated in three separate years, in contrast suggested that individuals grown on high quality trees possessed a significantly higher encapsulation rate compared to those on low quality trees.

This difference in the results is difficult to explain unambiguously. One notable observation was that in the laboratory there was no difference in pupal masses between individuals fed on high or low quality food, while in the field they were significantly higher in individuals reared on high quality trees. This may mean that in the laboratory study the quality difference between the leaves collected from high and low quality trees was less extreme than in the field study. Thus the seemingly contradictory results might be explained by a non-linear relationship between food quality and encapsulation reaction. Relatively mild food stress in the laboratory experiment might result in an enhanced encapsulation reaction, while extreme food stress in the field might dilute the strength of the immune defence. Other stress factors, such as pollution (Galloway & Depledge 2001) and crowding (Goulson & Gory 1995), have also been shown to act in a comparable manner in invertebrates.

In spite of the statistically significant differences in the encapsulation rate, the host resistance experiment using wild parasitoids in their natural environment showed similar vulnerabilities between the quality classes (**V**). For example, in 2006 an approximately six units (*ca*. 8 %) higher mean encapsulation score did not seem to significantly increase the resistance of the autumnal moth against larval parasitoids; almost all the larvae sampled were parasitized, in both quality classes (**V**). The tight co-evolutionary linkage between the autumnal moth and its parasitoids may explain why the parasitoids were able to overcome the immune defence of the autumnal moth. Another possibility is that more than just melanisation may be needed for successful encapsulation of the parasitoid egg. To conclude: differences in encapsulation ability did not straightforwardly correspond to resistance to naturally occurring hymenopteran parasitoids, indicating a minor role of the encapsulation response in the population level of the cyclic autumnal moth.

3.5. Immune defence and population density fluctuations

Haukioja (2005) suggested that grazing by the autumnal moth is involved in the defence of mountain birch and may trigger an increased immune defence in the herbivore leading to a low incidence of parasitism during the increase phase of the population cycle. Moreover, combining plant defence and parasitoid -mechanisms in this way could explain the cyclicity of autumnal moth populations (Haukioja 2005).

In study **VI**, differences in encapsulation ability were investigated for autumnal moth pupae grown as larvae at ten separate study sites, with different current and past larval densities and risks of parasitism. However, no obvious differences were found between the sites, giving no support for the hypothesis that the cycles of the autumnal moth are driven or modulated by variations in immune defence.

4. CONCLUSIONS

In spite of an enormous amount of field-work exploring the well thought out and widely accepted theories about the population cycles of herbivores, the reasons for most of the population cycles observed in nature are still unclear and lack scrutiny by crucial field experimentation. This may be due to the fact that biological systems with cyclic population dynamics are governed not by one but by a multitude of factors (Hanski 1987, Bonsall & Hassell 1995). While the results of this thesis give more support for the hypothesis suggesting the importance of hymenopteran parasitoids as drivers of population cycles of the autumnal moth (**I**, **II**), it is extremely difficult to demonstrate convincingly that the cycle is driven by a particular mechanism (e.g. one specific trophic interaction). In order to better understand the cyclic population dynamics of the autumnal moth, the effects of all contributing factors as well as their interactive effects in the system should thus be examined. For example, the interactive tri-trophic-level effects of the mountain birch, herbivores and natural enemies still need further study. Such a demonstration, however, requires a huge effort of experimental work on large spatial and temporal scales, as seen in the studies of snowshoe hares in Canada or voles in Fennoscandia (Krebs *et al.* 2001, Korpimäki *et al.* 2002).

A high number of complex interactions, direct or indirect, between trophic levels are thought to be important determining factors shaping ecological communities (Bukovinszky *et al.* 2008). Moreover, two-trophic-level approaches may provide only a partial view of communities, which are largely composed of more trophic levels (Price *et al.* 1980, Gomez & Zamora 1994, Schmitz *et al.* 2000, Bukovinszky *et al.* 2008, van Veen *et al.* 2008, Harvey *et al*. 2009). In the system studied, at least three trophic levels (host plant, herbivores and natural enemies) were found to interact with each other. There may in fact be a fourth level, consisting of hyper-parasitoids (i.e. parasitoids of parasitoids) (e.g. Harvey *et al.* 2009). Although I did not find any in my studies, some hyperparasitoids are found earlier from primary parasitoids of the autumnal moth (K.Ruohomäki unpubl. data). In my study system, primary parasitoids were found to have both direct and indirect top-down forces: they obviously affected the performance and abundance of the autumnal moths, but they also indirectly affected the grazing pressure confronted by the plant (**III**). The host plant was also found to affect the performance and level of immune defence of the autumnal moth, at least when the latter was measured via immune reactions against an artificial antigen (**IV**, **V**). However, exposure tests using wild parasitoids in their natural environment showed similar vulnerabilities to both larval and pupal parasitism independent of encapsulation ability (**V, VI**). The possible tight co-evolutionary linkage between the autumnal moth and its parasitoids may explain why the parasitoids were able to overcome the immune defence of the autumnal moth. When studying resistance to parasitoids, immunoassays

in laboratory may thus not be adequate; rather, host resistance experiments should be conducted with natural enemies.

As a conclusion to the whole thesis: my work offers a new, previously unknown perspective on the complex interactions occurring in the system studied. However, more two- and tri-trophic level studies, taking into account both direct and indirect interactions between and within trophic levels are still needed, in order to thoroughly understand the functions and roles of the different players at each trophic level. The population cycles of the autumnal moth may well be driven by hymenopteran parasitoids, but conducting crucial field experiments which unambiguously prove this is an extremely difficult and time-consuming matter. This remains a great challenge for future work, both empirical and model-based, preferably in combination.

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